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Citation for published version:

Gebruk, A, Zalota, AK, Dgebuadze, P, Ermilova, Y, Spiridonov, VA, Shabalin, N, Henry, L, Henley, SF & Mokievsky, VO 2021, 'Trophic niches of benthic crustaceans in the Pechora Sea suggest that the invasive snow crab *Chionoecetes opilio* could be an important competitor', *Polar biology*, vol. 44, no. 1, pp. 57-71. <https://doi.org/10.1007/s00300-020-02775-3>

Digital Object Identifier (DOI):

[10.1007/s00300-020-02775-3](https://doi.org/10.1007/s00300-020-02775-3)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Polar biology

Publisher Rights Statement:

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Trophic niches of benthic crustaceans in the Pechora Sea suggest that the invasive snow crab *Chionoecetes opilio* could be an important competitor

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Received: 28 February 2020 / Revised: 12 October 2020 / Accepted: 21 November 2020 / Published online: 8 December 2020
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Abstract

Expanding human activities alongside climate change, the introduction of invasive species and water contamination pose multiple threats to the unique marine ecosystems of the Pechora Sea in the Russian Arctic. Baseline data on biodiversity and responses to environmental change are urgently needed. Benthic decapod crustaceans are globally distributed and play an important role in fisheries, yet their roles in food webs are less understood. In this study, we used an integrated approach combining stomach content analysis and stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to examine the trophic niches of three decapod species in the Pechora Sea including the invasive snow crab *Chionoecetes opilio* and two species of native decapods, the spider crab *Hyas araneus* and the hermit crab *Pagurus pubescens*. Stomach contents of 75 decapods were analysed (*C. opilio* $n=23$; *H. araneus* $n=9$; *P. pubescens* $n=43$), and 20 categories of prey items were identified with the most frequently occurring prey items being bivalve molluscs (*Ciliatocardium ciliatum*, *Ennucula tenuis*, *Macoma calcarea*), polychaetes, crustaceans and plant debris. Bayesian ellipse analyses of stable isotope signatures ($n=40$) revealed that *C. opilio* displays an overlapping trophic niche with the two native decapods, providing direct evidence that the invader likely competes for food resources with both *H. araneus* and *P. pubescens*. As such, the presence of this invasive species could hold important consequences for trophic interactions, benthic ecosystem functioning and biodiversity. Microplastics were also found to be a likely stressor on this ecosystem, as 28% of all stomachs contained digested microplastics among other items. Long-term studies of benthic ecosystem structure and functioning are now needed to more fully understand the extent to which this new competitor may alter the future biodiversity of the Pechora Sea alongside the additional stressor of digested plastics.

Keywords *Chionoecetes opilio* · Pechora Sea · Stomach contents · Stable isotopes · Microplastics · Invasive species · Arctic Ocean · Benthic ecosystem

Supplementary Information The online version of this article (<https://doi.org/10.1007/s00300-020-02775-3>) contains supplementary material, which is available to authorized users.

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Introduction

Pechora Sea ecosystems: conservation priorities and challenges

Marine ecosystems of the Pechora Sea, in the south-eastern basin of the Barents Sea (Fig. 1), are characterised by a number of distinct features including relatively shallow water depths, significant impacts of continental runoff from the Pechora river, partial isolation from the open sea, a relatively short ice-free period, and a historically low level of anthropogenic activities (Nikiforov et al. 2005; Sukhotin et al. 2019). Several areas in the Pechora Sea have more recently been selected as components of a network of conservation priority areas in the Russian Arctic

due to their importance as feeding grounds for seabirds and marine mammals (Spiridonov et al. 2017; Denisenko et al. 2019a; Gebruk et al. 2020). However, rapid increases in human activities such as oil and gas extraction, shipping, tourism, combined with climate change, introduction of invasive species and the release of contaminants are predicted to have a cumulative impact on the unique marine ecosystems of the Pechora Sea (Sukhotin et al. 2019; Semenova et al. 2019). Recent assessments of the current state and future challenges of the Pechora Sea ecosystems (Sukhotin et al. 2019) highlighted the importance of biodiversity studies in providing baseline data for future conservation and sustainable management activities in the region. In particular, investigations of food webs and trophic relationships between species are important for better understanding of biodiversity and broader ecosystem functioning.

Ecological and trophic niche of benthic decapods

Benthic decapod crustaceans are globally distributed and play an important role in benthic ecosystems and in fisheries, especially in the Arctic region where fisheries are expanding as climate change and sea ice losses accompany ecosystem shifts (Grebmeier 2012; Kolts et al. 2013). Whilst commercially fished populations of some circumpolar benthic decapod species including the snow crab *Chionoecetes opilio* have been studied in detail within the harvested distribution range, their diets and trophic roles remain less understood (Divine et al. 2017). Early studies on cold-water crab feeding indicate that they are opportunistic feeders, consuming the most abundant benthic organisms, though usually one food group/species dominates their diet and this varies regionally (Kun and Mikulich 1954; Kulichkova 1955; Cunningham 1969; Tarverdieva 1981; Jewett et al. 1989).

Diets are often used to determine ecological niches with various indices available to estimate niche overlaps, such

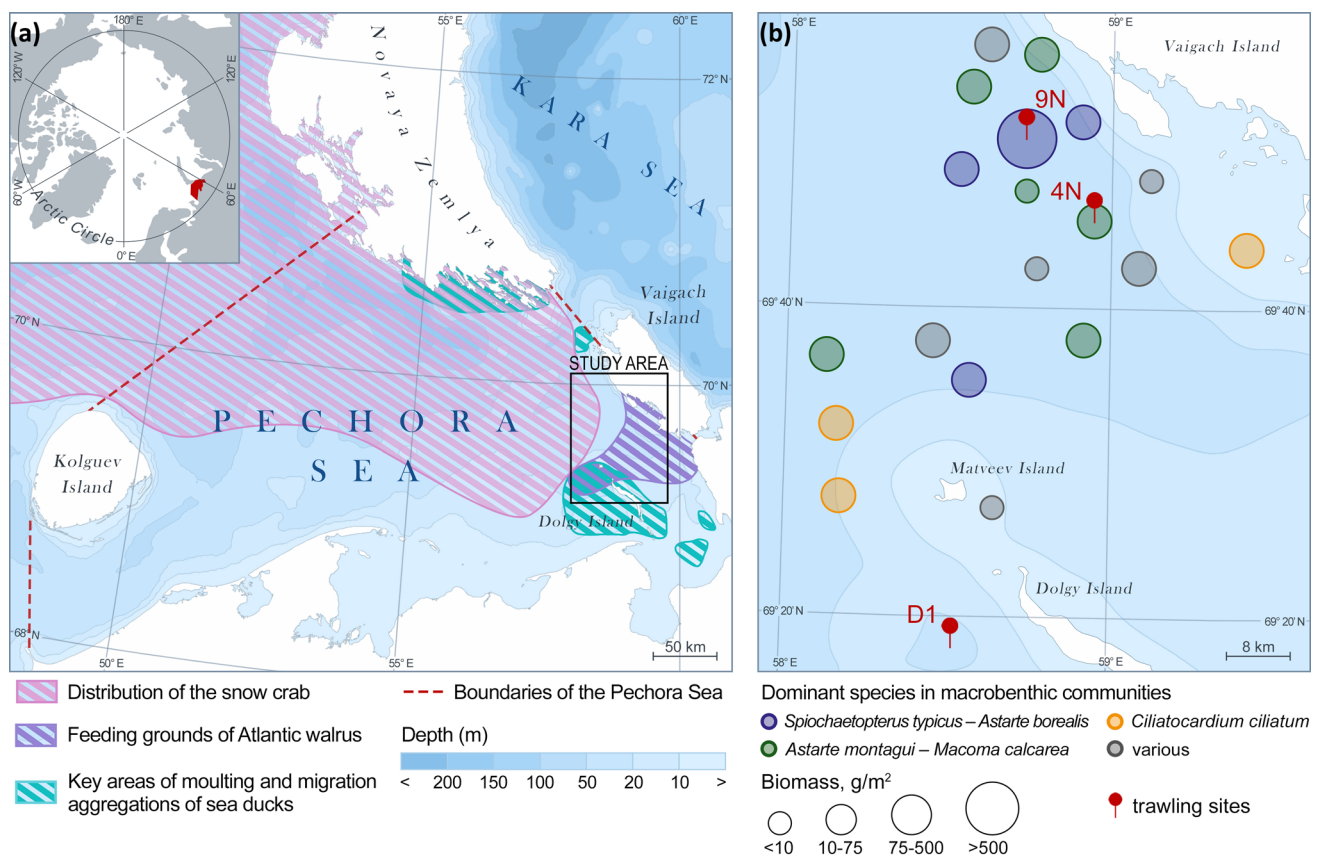


Fig. 1 **a** Overview map showing position of the study area in the Pechora Sea and in the broader Arctic. Pink dashing shows distribution of the snow crab in the research area (Lorentzen et al. 2018); purple dashing marks feeding grounds of Atlantic walrus (Semenova et al. 2019; Gebruk et al. 2020); green dashing corresponds to the

key moulting and migrating areas of sea ducks (Sukhotin et al. 2008). **b** Detailed map of the sampling area: trawling sites are shown with red pins; circles of different colours represent biomass of dominant species in macrobenthic communities (Gebruk et al. 2020)

as the Pianka's measure, MacArthur and Levins' measure, Morista's measure and others (Kerbs et al. 2017). Similarly, the composition of stable isotopes of carbon and nitrogen in animal tissues is used in feeding ecology as an emergent property of dietary niches and habitat use (Post 2007; Flaherty and Ben-David 2010). This is because carbon/nitrogen ratios in the tissues of aquatic organisms provide information on the source of feeding ($\delta^{13}\text{C}$) and relative trophic position ($\delta^{15}\text{N}$) (Linnebjerg et al. 2016; Odintsov and Kiyashko 2018). The term 'isotopic niche' (Newsome et al. 2007) is broadly used in stable isotope analyses. It is defined as an area in $\delta^{13}\text{C}/\delta^{15}\text{N}$ space that characterises the trophic resources and habitat use of the species.

In the present study, we compared overlap in dietary niches determined by stomach content analyses with overlap in isotopic niches based on stable isotope analysis to gain a better understanding of the trophic relationships between the three benthic decapod species in the Pechora Sea: the invasive snow crab *Chionoecetes opilio* and two native benthic crustaceans, the spider crab *Hyas araneus* and the hermit crab *Pagurus pubescens*. These three decapod species now form a guild of predators/scavengers at the top of the food web in the benthic ecosystem of the Pechora Sea.

Distribution and diets of *C. opilio*, *H. araneus* and *P. pubescens*

The snow crab *C. opilio* is a stenothermal brachyuran species broadly distributed in the northern Pacific and northern Atlantic Oceans, but in the Pechora Sea, it is an alien invasive species (Alvsvåg et al. 2009; Sokolov et al. 2016; Mullowney et al. 2018; Zalota et al. 2018). *C. opilio* was first recorded in fisheries bycatch in the Barents Sea near Gusi-naya Banka in 1996, thereafter forming a self-maintained population; however, it was not deliberately introduced to the area (Jørgensen and Spiridonov 2013; Sokolov et al. 2016; Mullowney et al. 2018). It is a boreal Arctic cold-water species, typically inhabiting muddy sand grounds in waters 150–250 m deep in the Barents Sea (Bakanev et al. 2016). Average commercial size for male *C. opilio* in the Barents Sea is 113.8 mm carapace length (CL) and 58.7 mm carapace width (CW) (Bakanev and Pavlov 2019). In the Pechora Sea, *C. opilio* is most abundant near the Yuzhny Island of Novaya Zemlya archipelago (Zalota et al. 2018), where water masses are influenced by cold Arctic water from the Kara Strait (Bakanev et al. 2016; Zalota et al. 2018).

Several previous studies on diets of *C. opilio* were mostly conducted in Atlantic Canada (Miller 1981; Brethes et al. 1982; Wieczorek and Hooper 1995; Squires and Dawe 2003), with some studies in the Pacific Arctic (Chuchukalo et al. 2011; Divine et al. 2017), the North Pacific (Tarverdieva 1981; Nadtochiy et al. 2004), and in the Barents Sea (Manushin et al. 2016; Zakharov et al. 2018). Studies on

C. opilio diets have all reported diverse diets and the main food items varying between locations: polychaetes and crustaceans near the northeastern Newfoundland shelf (Squires and Dawe 2003); polychaetes and bivalves near the east coast of Newfoundland (Miller 1981); and fish near Bonne Bay, off the west coast of Newfoundland (Wieczorek and Hooper 1995). In this last case, authors hypothesised scavenging of discarded bait as the main foraging activity of snow crabs (Wieczorek and Hooper 1995). In the Barents Sea, adult males live deeper and consume more polychaetes and crustaceans that are more dominant on bank slopes. Females and subadult males show significant consumption of molluscs dominant in shallower areas, which they mostly inhabit (Zakharov et al. 2018). Most early studies agree on polychaetes, molluscs, crustaceans and echinoderms being present in diets of snow crabs, but with variable frequencies of occurrence in stomachs depending on species composition of the local macrobenthos.

The great spider crab *Hyas araneus* is a benthic decapod species widely distributed in the boreal North Atlantic and adjacent Arctic seas (d'Udekem d'Acoz 1999). It is the most common native brachyuran crab in the Barents Sea found in intertidal, upper and lower subtidal zones (Kuznetsov 1964; Zimina et al. 2015). The hermit crab *P. pubescens* is an Arctic-Boreal species, also common in the Barents Sea. It usually dwells in the shells of *Buccinum*, *Neptunea* and other gastropods, and is relatively small in size compared to both *C. opilio* and *H. araneus*, its body length not exceeding 100 mm (Gaevskaya 1948; d'Udekem d'Acoz 1999).

The diets of *H. araneus* and *P. pubescens* have not been extensively studied. *H. araneus* is known as a predator, very rarely consuming food items of plant origin, but more actively feeding on a broad range of benthic, hyperbenthic and planktonic animals. These include hydroids, loricates, gastropods, bivalves (including juveniles of scallops and mussels), amphipods, copepods, euphausiids, small crabs, sea stars, brittle stars, juvenile sea urchins and fishes (Squires 1990; Arsenault and Himmelman 1996; Fagerli et al. 2013; Pushkina 2017). Fatty acid studies in Spitsbergen showed that *H. araneus* in that region consume mostly benthic seston-feeding invertebrates (Paar et al. 2019) and even zooplankton (Legeżyńska et al. 2014). These food sources were also indicated by stable isotope analysis of the trophic status of this species in the southern Barents Sea fjords (Zalota 2017; Spiridonov et al. 2020).

In the Atlantic waters off Canada, *P. pubescens* is known to feed on phytobenthos, foraminifera, amphipods, ostracods, hydroids, fragments of bivalves, polychaetes and brittle stars (Squires 1990). In the Kongsfjord of Spitsbergen (Paar et al. 2019) and the fjords of the southern Barents Sea (Zalota 2017; Spiridonov et al. 2020), *P. pubescens* occupies a somewhat lower trophic level than *H. araneus*. There is also evidence that *P. pubescens* can

consume plant material of terrestrial origin in the areas of abundant ornithogenic coastal vegetation in Spitsbergen (Zmudczyńska-Skarbek et al. 2015).

Macrobenthos of the Pechora Sea: foraging resources for benthic decapods

Macrobenthic communities of the Pechora Sea that form the bulk of benthic decapod diets in the study area are generally well described in the literature from the 1920s (Brotskaya and Zenkevich 1939) with more detailed surveys conducted in the 1990s (Denisenko et al. 2003; Kucheruk et al. 2003). Macrobenthos of the Pechora Sea are characterised by very high spatial variability in terms of species composition and biomass, their distribution being controlled by substrate type, bottom topography and larger scale oceanographic regimes (Denisenko et al. 2003). Average biomass of macrobenthos in the Pechora Sea ranges from 1.5 to 536 g wet weight per m² (Denisenko et al. 2003). The shallows of Pechora Bay are characterised by particularly low biomass (Gebruk et al. 2019; Denisenko et al. 2019b), whilst the north-western parts near the Novaya Zemlya and Vaygach Islands have the highest values of biomass of macrobenthic invertebrates in the Pechora Sea with largest contributions formed by bivalve molluscs *Astarte borealis*, *Ciliatocardium ciliatum*, *Serripes groenlandicus*, *Nicania montagui* and *Macoma calcaria* (Denisenko et al. 2019a; Gebruk et al. 2020). The presence of *C. opilio* and predation on benthic invertebrates may have an impact on the structure of these macrobenthic communities in the Pechora Sea, and may also go on to affect the availability of benthic feeding resources for seabirds (i.e. common eiders and other sea ducks) and marine mammals that forage on the benthos here including Atlantic walrus (*Odobenus rosmarus*; Gebruk et al. 2020) of the endangered Pechora Sea population (walrus listed as Vulnerable in the International Union for Conservation Red List, IUCN 2016).

Objectives and expectations of this study

Despite growing scientific and industrial attention on the Pechora Sea, our understanding of the Pechora Sea food web and trophic relationships between species remains limited, and in particular, the extent to which the spread of *C. opilio* may impact these relationships and alter biodiversity. When assessing diet composition and trophic niches of the three decapod species in this study, we expected *H. araneus* and *P. pubescens* to occupy distinct feeding niches due to their assumed long species co-existence and food resource partitioning (similar processes of niche separation have been described in some

other decapod assemblages, e.g. Cartes 1998). At the same time, we expected the invasive species, *C. opilio*, to occupy overlapping dietary niches with *H. araneus* and *P. pubescens* as result of interference competition with the native decapods (Boudreau and Worm 2012). Combination of diet assessment with stable isotopic analysis used in this study is aimed to improve understanding of ecological and trophic niche of *C. opilio* in the Pechora Sea and inform future management and policy decisions leading to prevention of potential trophic shifts and biodiversity loss in the region.

Methods

Study area

Samples were collected during the R/V *Kartesh* cruises to the Pechora Sea in 2017–2018 in the area between the Vaygach and Matveev Islands in the south-western part of the sea at the depth range 18–39 m (Fig. 1). The study area lies within the important feeding grounds of Atlantic walrus (Semenova et al. 2019; Denisenko et al. 2019a; Gebruk et al. 2020), and marine duck species, including kind eiders, black and velvet scoters (Sukhotin et al. 2008). According to previous benthic surveys, macrobenthos in the area is formed by diverse communities of 133 species of invertebrates (Gebruk et al. 2020). Macrobenthic biomass is predominately formed by bivalve astartid molluscs (with the biggest contributions from *Astarte borealis*, *Astarte montagui* and *Ciliatocardium ciliatum*), but it varies greatly ranging from 32 g m⁻² (site 4 N) to 500 g m⁻² (site 9 N) (Gebruk et al. 2020) (Table 1, Fig. 1). Presence of the decapod species *C. opilio*, *H. araneus* and *P. pubescens* in the research area was previously noted based on remotely operated vehicle (ROV) video footage (Gebruk et al. 2020), but their diets and trophic roles have not been studied. Bottom sediments are mostly homogeneous and formed by silty sands (Denisenko et al. 2019a; Gebruk et al. 2020).

Sample collection

Samples of benthic decapods for this study were collected from two sites in 2017 (9 N and 4 N) and three sites in 2018 (9 N; 4 N; D1) using a *Sigsbee* bottom trawl with a 1.5-m length frame and 0.5 mm mesh, manufactured in the Shirshov Institute of Oceanology, Moscow. Trawling was conducted at 2 knots for 30 min corresponding to a linear 1.85 km transect.

Bottom sediments from trawl catches were washed over a 0.5 mm mesh with seawater. Individuals of the decapod

Table 1 Positions of trawling sites (taken at the beginning of a transect), depths and key characteristics of macrobenthic communities: biomass (g m⁻²), number of species, dominant species

Site no.	Coordinates (degrees and decimal minutes)		Depth (m)	Biomass (g m ⁻²)	Number of species	Dominant species
9 N	N69;50.727'	E058;45.804'	39	522.78	45	<i>Astarte borealis</i>
4 N	N69;45.635'	E058;57.347'	28	32.28	49	<i>Astarte montagui</i>
D1	N69;17.809'	E58;30.986'	18	n/a	n/a	n/a

species *C. opilio*, *H. araneus* and *P. pubescens* were then manually extracted and preserved for the further analyses. Individuals used for stomach content analysis (collected in 2017) were preserved in 4% formaldehyde solution, and then dissected in a laboratory. Extracted stomachs were transferred into 70% ethanol. Individuals used for isotopic analyses (collected in 2018) were measured and frozen at - 20 °C. All crabs were thawed, blotted with paper filters, and weighed prior to dissecting to the nearest 0.01 g (wet weight). Their sex was identified and carapace length (CL) and width (CW) were measured to the nearest 0.01 mm with digital Vernier calipers (data provided in supplementary material, Online Resource 1).

Stomach content analysis

Seventy-five decapods collected in 2017 were used for stomach content analyses, of which 23 were *C. opilio*, nine were *H. araneus* and 43 were *P. pubescens*. Stomachs were dissected and their contents visually examined under a stereomicroscope. All items found in stomach contents were categorised into prey items (digestible remains of animals, unidentified organic debris) and other items. Prey items were identified to the lowest possible taxonomic level. Partly digested matter with no preserved hard structures that could be used for species identification were divided into 'plant debris' (remains of algae or aquatic plants with structures like blades or rhizoids) and 'organic debris' (digested amorphous material or detritus). Inclusions included sand, feathers and microplastics. Microplastics were defined as non-digested fibres or particles < 5 mm in length made of firm synthetic materials, often brightly coloured (Avio et al. 2017).

Food lump analysis was carried out following Burukovsky (2009). For each stomach, level of fullness was estimated visually and only stomachs that were > 25% full were used for food lump reconstructions. For each item in a stomach (prey items only), the percentage volume in the food lump was estimated visually. Based on average percentage volumes, a so-called 'virtual food lump' (Burukovsky 2009) was then reconstructed for each species to characterise diets. Besides level of fullness and prey species composition, other indices included: (1) dominance (as percentage of stomachs where a single prey

item comprised > 60% of the food lump of all stomachs of species) and (2) mean number of prey items per stomach for each species. In addition, a matrix of presence-absence of each prey item in each stomach was constructed. Presence-absence data were used to calculate frequencies of occurrence of each stomach content component in diets of each species (as percentage of stomachs where this item was present).

To assess the predicted number of species in the diet of each species of decapod, species accumulation curves were calculated using the species richness (S) of diet components with the *Chao-2* type estimator as the following:

$$\tilde{S} = S_{obs} + \frac{(H-1)s_1^2}{2Hs_1},$$

where H = samples, S_{obs} = the total number of observed species (diet components) and S_1 = the number of species (diet components) found in exactly one stomach.

Pianka's overlap measure (Pianka 1974) was used to assess overlaps in feeding niches based on frequencies of occurrence of feeding items following Krebs (1998):

$$O_{jk} = \frac{\sum_i^n p_{ij}p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}},$$

where O_{jk} is the Pianka's measure of niche overlap between species j and species k , p_{ij} proportion resource is one of the total resources used by species j (occurrence of feeding item); p_{ik} proportion resource is one of the total resources used by species k ; n = total number of resources (feeding items).

To assess the relationships between the three species diets in more detail, we used the non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity index and cluster analysis based on an unweighted pair group method with arithmetic mean (UPGMA) algorithm. Similarity of percentages (SIMPER) analyses was then carried out to assess contributions to differences between diets of different species. A pairwise analysis of similarities (ANOSIM) was performed, yielding pairwise comparisons of these and their associated p values, with sequential Bonferroni corrections applied. All statistical calculations were performed

using free statistical software PAST version 3.22 (Hammer and Harper 2006).

Stable isotope analysis

In August 2018, specimens of decapods were collected for stable isotope analysis at three stations in the Pechora Sea (9 N, 4 N and D1, Fig. 1). Muscle tissue from their claws was extracted in the laboratory and dried in plastic vials at 70 °C for 3 days. Dry tissue was then crushed into powder using a pestle and mortar and packed in tin foil (200–500 µg each). The isotopic analysis was carried out using a Thermo Delta V Plus isotope ratio mass spectrometer and Thermo Flash1112 element analyser at the Center for Collective Use at the Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (SIEE RAS).

The ratios of the stable isotopes of carbon and nitrogen ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) are presented in the delta per mille notation (δ , ‰) relative to international standards (VPDB for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$). The analytical error in determining the isotope composition (SD in the laboratory standard analysis, $n=6$ to 8) did not exceed 0.2‰. The $\delta^{13}\text{C}$ values have been corrected for lipid concentration according to Post et al. (2007, their formula 3) for samples with mass C/N ratio higher than four.

Data were tested for normality using Shapiro–Wilk test and Levene’s test for homogeneity to confirm if parametric tests can be used for further comparison. Differences in the isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the three decapod species used in this study were tested using analysis of variance (ANOVA) with species and sampling area as factors. Isotopic niche parameters were calculated using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011) using RStudio (RStudio Team 2016; R Core Team 2018). The area of standard ellipses corrected for small sample size (SEA_C) and their posterior estimates (SEA_B) were used to compare individual species. The overlap of SEA_C (including 95% of the data) was used to discuss isotopic niche proximity of different species. These overlaps were compared to the posterior distribution of SEA_B overlaps to control for sample size errors. The overlap was reported as the proportion of the non-overlapping area (the total overlap area divided by the sum of the areas of two ellipses minus the total overlap area in ‰²).

Results

Stomach content analysis

Collected crabs were a mixture of males and females with a predominance of males in all three species: 13 males and 10 females of *C. opilio*; 7 males and 2 females of *H. araneus*;

32 males and 11 females of *P. pubescens* (Supplementary material, Online Resource 1). All *C. opilio* were smaller than the average size of commercially exploited adults in the Barents Sea (113.8 mm CL, Bakanev and Pavlov 2019). Noticeably *C. opilio* and *H. araneus* were of a similar size group: *C. opilio* average CL was 32.0 ± 3.75 mm, ranging from 27 to 32 mm; *H. araneus* average CL was 47.0 ± 8.44 mm (28–58 mm); and *P. pubescens* were 4–5 times smaller with CL of 8.5 ± 2.62 mm (4.0–12.5 mm).

Approximately 22% of all stomachs were empty or near-empty (< 25% fullness), comprising two stomachs of *P. pubescens* (out of 43), three stomachs of *H. araneus* (out of 9) and 11 stomachs of *C. opilio* (out of 23). The rest contained prey items and were identified as full or near-full (> 75% fullness) or not empty (25–75%) (supplementary material, Online Resource 1). All stomach contents reflected mixed diets with an average of 6 prey items (5 ± 1.8 for *C. opilio* and *H. araneus*; 6 ± 1.2 for *P. pubescens*). Low value of dominance index (3%) showed that few food lumps were dominated by only one prey item (excluding organic debris).

Nineteen categories of items were identified in stomach contents, 15 of which were classified as prey items. Twenty-seven taxa of benthic invertebrates were identified (12 to species level, 5 to genus, rest to family or above). A full list of prey items is presented in Online Resource 2. With respect to species richness, bivalve molluscs, annelids and foraminifers were the most diverse groups, accounting for 5 to 6 taxa each. Most of the other taxonomic groups were represented by a single species or by unidentifiable fragments. Identified bivalves included *Astarte elliptica*, *Mytilus edulis*, *Ciliatocardium ciliatum*, *Dacrydium vitreum*, *Ennucula tenuis* and *Macoma calcaria*. Identified annelids (polychaetes) included *Pectinaria* sp., *Nephtys* sp., *Owenia* sp., Maldaniidae, Cirratulidae and Aphroditiformia.

The most frequently occurring prey items in food lumps, excluding organic debris, were bivalve molluscs and annelids for *C. opilio* and *H. araneus*, in addition to plant debris for *P. pubescens* (Fig. 2). Crustaceans (amphipods or barnacles) were represented in > 10% of stomachs of each species, whilst the frequency of occurrence of all other prey items varied significantly between the three decapod species (Fig. 2). Food lumps of *H. araneus* had relatively small numbers of prey items (6 excluding detritus and inclusions), and each was present in > 10% of stomachs, as opposed to *P. pubescens* and *C. opilio* that had a larger variety of prey items (10 to 13) with variable frequencies of occurrence ranging from 2 to 83%.

Noticeably, smaller animal taxa were more frequent in stomachs of *P. pubescens* than in other decapods. For example, foraminifers (*Cibicides refulgens*, *Elphidium excavatum*, *Buccella frigida* and others) were found in 37% of *P. pubescens* stomachs, 9% of *C. opilio* and 1% of *H. araneus*. Similarly, hydrozoans (*Obelia* sp. and others) were present

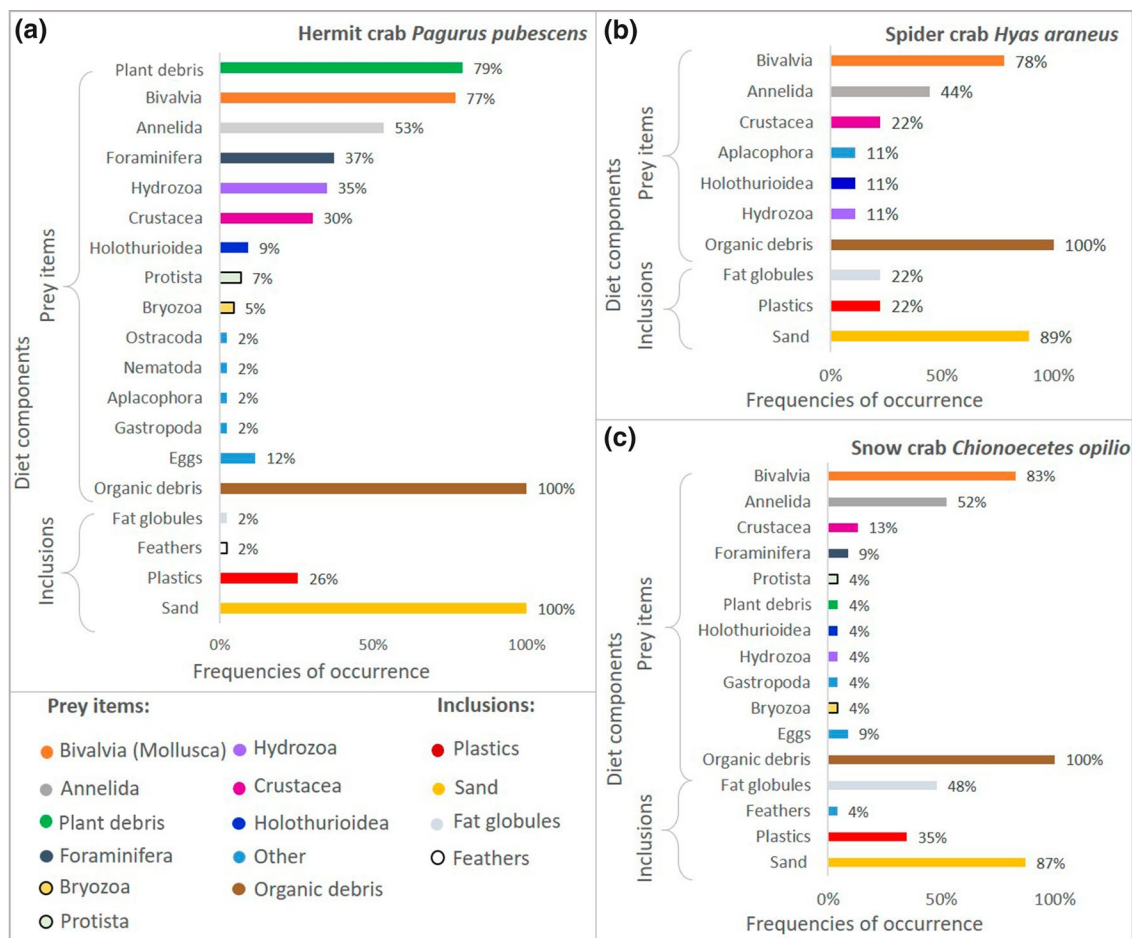


Fig. 2 Frequency of occurrence (%) of diet components in stomachs of *P. pubescens* (a); *H. araneus* (b) and *C. opilio* (c)

in 35% of *P. pubescens*, 11% of *H. araneus* and only 4% of *C. opilio*. Nematodes and ostracods were only present in stomachs of hermit crabs.

Sand granules were present among the inclusions in the majority of stomachs of all species with a 92% average frequency of occurrence (ranging from 87% for *C. opilio* to 100% for *P. pubescens*). Microplastics occurred with 27% average frequency, ranging from 22% for *H. araneus* to 35% for *C. opilio* (Online Resource 3). Organic debris appeared in all non-empty stomachs of all species (100% frequency of occurrence). Similarly, organic debris played an important role in food lumps of all three species. However, its relative contribution to the total volume as well as contribution of other prey items and inclusions varied between species (Fig. 3).

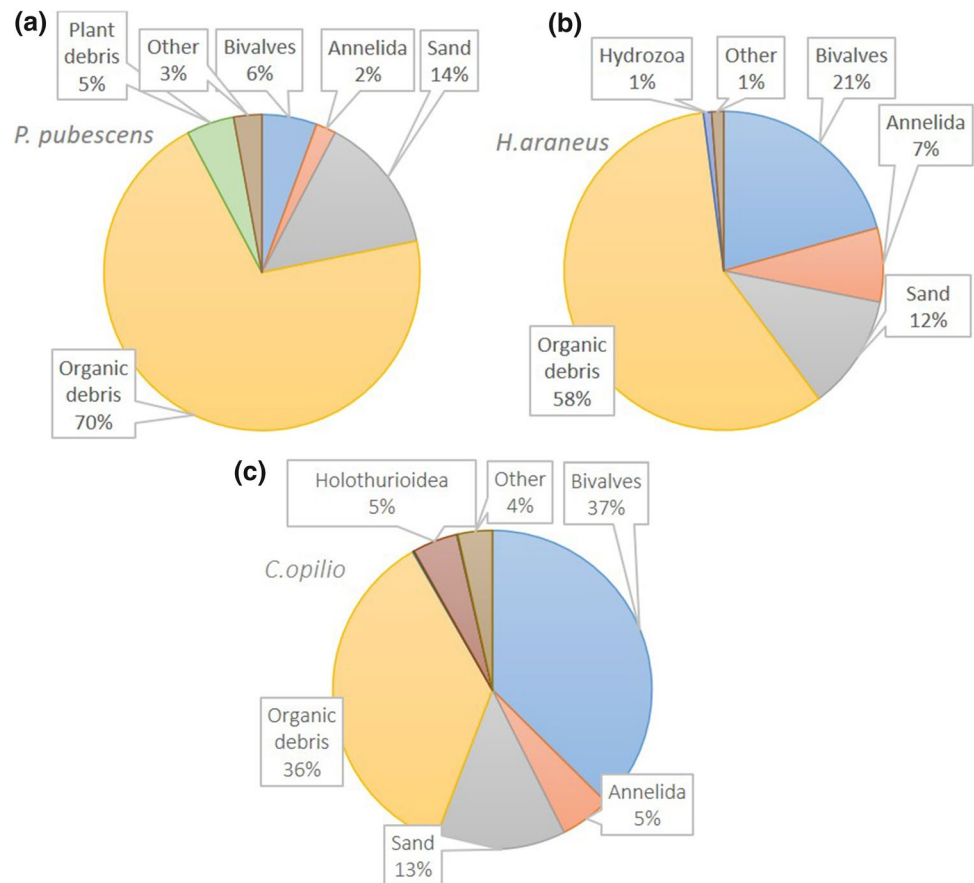
In the food lump of *P. pubescens*, organic debris accounted for 70% of total volume, followed by sand granules (14%), bivalve molluscs (6%), plant debris (5%), and other prey items that together only accounted for 3% of the volume. The food lump of *H. araneus* also consisted primarily of organic debris (58% of the total volume), followed by

bivalve mollusc (21%), sand granules (12%), polychaetes (7%), with minor contributions from hydrozoans (1%) and other groups (1%). In contrast, bivalve molluscs (37%) were key contributors to the total volume of the food lump of *C. opilio* followed by organic debris (36%), sand (13%), polychaetes (5%), holothurians (5%), and other groups (together accounting for 4% of the total volume).

Neither UPGMA hierarchical cluster analysis nor nMDS revealed strong differences between the three species. This shows that the diets of the three species overlap. It also appeared that *P. pubescens* tended to separate more from *C. opilio* and *H. araneus* than *C. opilio* and *H. araneus* between each other (Fig. 4). Sex and predator size did not affect diet composition as determined by cluster and nMDS analyses.

For all pairs of species, Pianka's measure (calculated for frequencies of occurrence of prey items) was close to 1.0, representing almost full overlap in feeding resources. However, overlap between *C. opilio* and *H. araneus* (0.97) was higher than between *P. pubescens* and brachyuran crabs (0.75 for *C. opilio*–*P. pubescens* and 0.77 *H. araneus*–*P. pubescens*). Pairwise comparison of diets of the three

Fig. 3 Food lumps with relative proportions (%) of key prey items to total volume for *P. pubescens* (a) *H. araneus* (b) and *C. opilio* (c)



species using ANOSIM and Bray–Curtis similarity measure both agreed with Pianka's index suggesting close proximity between diets of *C. opilio* and *H. araneus* (0.67 similarity measure and no significant difference ($p > 0.05$) according to ANOSIM). However, they disagreed with the overlap measure in assessing the relationship between *P. pubescens* and other decapods: Bray–Curtis and ANOSIM showed low similarity and significant difference between *P. pubescens* and larger decapods (Table 2). Overall prey item compositions of *C. opilio* and *H. araneus* diets were close to each other, whilst stomach contents of *P. pubescens* were slightly different from both other species.

Species accumulation curves were used to assess cumulative numbers of prey items in the diets of the three species. The most diverse diet was in *P. pubescens*, comprising all 19 categories of discovered items, followed by *C. opilio* (16 categories) and *H. araneus* (11 categories). However, species accumulation curves showed that in fact *C. opilio* acquired diet components faster than two other species, with predicted increase in the number of stomachs increasing the number of prey items. This was confirmed by the Chao-2 estimator calculated for predicted total number of prey items. The expected values were: 33 for *C. opilio*, 18 for *H. araneus* and 27 for *P. pubescens*. Conversely, accumulation curves for *P. pubescens* were close to reaching a plateau

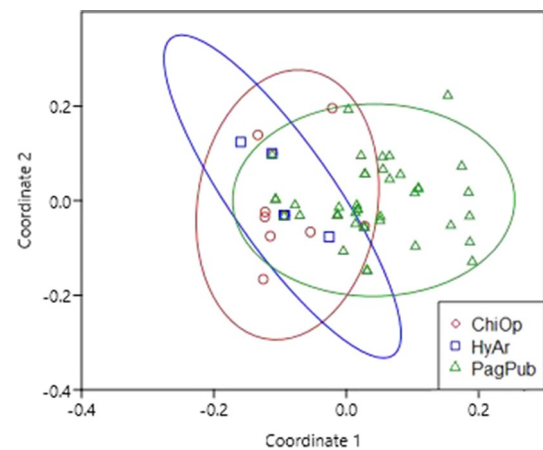
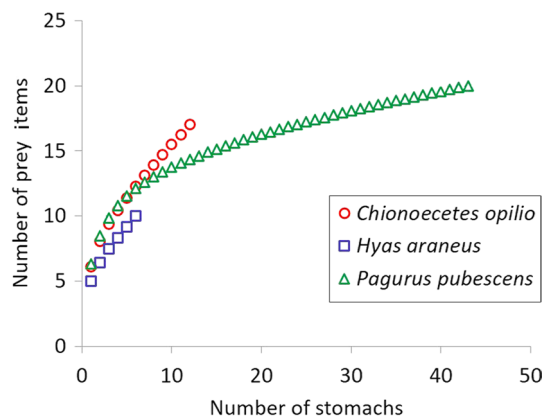


Fig. 4 Stomachs of different species grouped by the nMDS (95% ellipses), calculated with Bray–Curtis similarity measure. Stomach of *C. opilio*—red circles; *H. araneus*—blue squares, *P. pubescens*—green triangles

for the given number of stomachs (Fig. 5). Mean increment rate of the number food items was the highest for *C. opilio*, exceeding that both for *H. araneus* and *P. pubescens* at all the levels of sampling sets. These estimations confirm the

Table 2 Pairwise comparison of diets of three species with Pianka's niches overlap measure; Bray–Curtis similarity measure and ANOSIM analysis ($p < 0.05$ showed with green shading)

	Index value
Pianka's niches overlap index	
<i>C. opilio</i> – <i>H. araneus</i>	0.97
<i>C. opilio</i> – <i>P. pubescens</i>	0.75
<i>H. araneus</i> – <i>P. pubescens</i>	0.77
Bray–Curtis similarity measure	
<i>C. opilio</i> – <i>H. araneus</i>	0.67
<i>C. opilio</i> – <i>P. pubescens</i>	0.27
<i>H. araneus</i> – <i>P. pubescens</i>	0.39
ANOSIM (significance of difference based on Bray–Curtis similarity index)	
<i>C. opilio</i> – <i>H. araneus</i>	$p = 0.39$; $R = 0.01$
<i>C. opilio</i> – <i>P. pubescens</i>	$p = 0.001$; $R = 0.81$
<i>H. araneus</i> – <i>P. pubescens</i>	$p = 0.004$; $R = 0.46$

**Fig. 5** Species accumulation curves of *C. opilio*—red circles; *H. araneus*—blue squares, *P. pubescens*—green triangles

wider trophic niche of newcomer *C. opilio* in comparison with native species.

Table 3 Number of specimens (n), average $\delta^{13}\text{C}$ and $\delta^{15}\text{N} \pm$ standard deviation (means, ‰), and ellipse's area corrected for small sample size (SEA_C , ‰ 2) that includes 95% of the data. In brackets is the

	All (9 N, 4 N, D1)			9 N			4 N		
	n	Means	SEA_C	n	Means	SEA_C	n	Means	SEA_C
<i>C. opilio</i>	12	-20 ± 0.3 12.5 ± 0.4	0.46	6	-20 ± 0.3 12.7 ± 0.3	0.33	5	-19.8 ± 0.4 12.4 ± 0.3	0.50
<i>H. araneus</i>	10	-20.5 ± 0.3 12.3 ± 0.5	0.36				10	-20.5 ± 0.3 12.3 ± 0.5	0.36
<i>P. pubescens</i>	18	-19.8 ± 0.3 11.9 ± 0.5	0.42	8	-20 ± 0.5 11.5 ± 0.5	0.27 (0.47)	8	-19.7 ± 0.2 12.4 ± 0.3	0.15

All data include samples from D1 sampling area

Stable isotope analysis

Overall 40 decapods were used in stable isotope analysis of which 12 were *C. opilio* (six from Station 9 N, five from 4 N, and one from Station D1); 10 *H. araneus* (all from Station 4 N); and 12 *P. pubescens* (eight from Station 9 N, eight from 4 N, and two from Station D1) (Table 3). ANOVA showed differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ when the samples from different areas were pooled as one (Table 4). The data were not normally distributed allowing the use of ANOVA (Shapiro–Wilk test; $p > 0.05$) and homogenous (Levene's test, $p > 0.05$). When parametric tests and SIBER analysis were performed on the data with sample area differences, the three crabs from nearby Dolgy Island (D1) were excluded due to low sample size (resulting in 37 crabs in total). ANOVA revealed differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between species and area, as well as an interaction among species and area for $\delta^{15}\text{N}$ data (Table 4).

Tukey's HSD test revealed differences in $\delta^{13}\text{C}$ between *H. araneus* versus *C. opilio*, and *H. araneus* versus *P. pubescens* ($p < 0.05$); and a difference only between *C. opilio* and *P. pubescens* in $\delta^{15}\text{N}$ (Table 5) in both ANOVA tests. In addition, Tukey's HSD test of the two-way ANOVA revealed differences between *H. araneus* with other decapod species in $\delta^{13}\text{C}$, and general difference between two areas and *P. pubescens* between the areas and with *C. opilio* for $\delta^{15}\text{N}$ data (Table 5).

The area of ellipses that incorporated 95% of the data, corrected for small sample size (SEA_C), are reported in Table 4 and presented in Fig. 6. Most of SEA_C were very similar to posterior estimate (SEA_B) except for the *P. pubescens* from 9 N where the mean SEA_B was twice the size of SEA_C ; however, the mode SEA_B (0.34) was somewhere between the two (which could be seen as a result of limited sample size and should be considered with caution). The proportion overlap of isotopic niches is presented in Table 6. The lowest overlap was between *H. araneus* and *P. pubescens* without area differentiation (0.08) and even more so when *P. pubescens* only from 4 N was considered (0.03).

average ellipse area of posterior estimate (SEA_B) for *P. pubescens* from 9 N (the only posterior estimate that was more than 0.02‰^2 different from SEA_C)

Table 4 Results of ANOVA test for data pooled by species with no area differentiation (pooled data) and two-factor ANOVA with species and area difference; as well as Shapiro–Wilk normality test and Levene’s test for homogeneity results for both types of ANOVA for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data

	ANOVA			Shapiro–Wilk normality test		Levene’s test for homogeneity		
	Df	F	p	W	p	Df	F	p
$\delta^{13}\text{C}$								
Pooled data	2	11.4	<i>0.0001</i>	0.97	0.33	2	0.43	0.65
Area differentiated data								
By species	2	13.1	<i>6.80E–05</i>	0.97	0.40	4	1.7	0.18
By sample area	1	3.7	<i>0.0644</i>					
Interaction species: area	1	0.2	0.6517					
$\delta^{15}\text{N}$								
Pooled data	2	4.7	<i>0.0153</i>	0.97	0.46	2	0.6	0.55
Area differentiated data								
By species	2	7.2	<i>0.0027</i>	0.97	0.41	4	0.9	0.47
By sample area	1	6.1	<i>0.0189</i>					
Interaction species: area	1	12.8	<i>0.0011</i>					

Statistically significant results ($p < 0.05$) shown in italics

Similarly low overlap was found between *C. opilio* and *P. pubescens* at 9 N.

Overall, stable isotope analysis showed a clear discrepancy of isotopic niches between *H. araneus* and *P. pubescens*, provided that within one station niches overlapped less than among all samples. The isotopic niches of *C. opilio* overlapped with both native decapod species to a greater extent.

Discussion

Trophic niches of *C. opilio*, *H. araneus* and *P. pubescens* in the Pechora Sea

From the present integrated study using both stomach contents and stable isotope analyses, it is clear that the diets

and trophic niches of the three decapod species *C. opilio*, *H. araneus* and *P. pubescens* overlap substantially and over time if the density and distribution of *C. opilio* continue to grow, this could threaten the structure and functioning of the benthic Pechora Sea ecosystem. The overall however is not surprising, considering similar feeding habits and co-occurrence in the same feeding grounds, with all three decapods being benthic omnivores that forage on macrobenthic communities. Co-occurrence of the two native Barents Sea species (*H. araneus* and *P. pubescens*) was previously reported during a field observation experiment on scavenging behaviour of *H. araneus* near Spitsbergen (Svalbard). However, during that experiment, *P. pubescens* individuals were near the bait (cod) but no scavenging activity was observed, whereas *H. araneus* actively consumed the bait (Markowska et al. 2008). This can be considered as circumstantial evidence that *H. araneus* and *P. pubescens* do not share carrion prey.

It is also not surprising that stomach content and isotopic composition in the same species can vary between stations (such as $\delta^{15}\text{N}$ values in *P. pubescens* at 9 N and 4 N), because macrobenthos of the Pechora Sea is highly variable over short spatial scales (Denisenko et al. 2003; Sukhotin et al. 2019). In the research area, the station 4 N is characterised by high biomass of macrobenthos with strong dominance of the bivalve mollusc *A. borealis*, whilst macrobenthos at station 9 N is formed by *A. montagui*–*M. calcarea* assemblage and characterised by low biomass (Gebruk et al. 2020).

Prey item composition of stomach contents showed that the diets of all three species consisted of bivalve molluscs and polychaetes with minor contributions from other taxa. Noticeably, the most frequent bivalve fragments in the stomachs (*C. ciliatum*, *E. tenuis*, *M. calcarea* and others)

Table 5 Results with significant difference ($p < 0.05$) of Tukey’s HSD test for two-factor ANOVA with species and area difference for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data

	p
$\delta^{13}\text{C}$	
<i>H. araneus</i> vs. <i>C. opilio</i>	0.0019
<i>H. araneus</i> vs. <i>P. pubescens</i>	0.0001
<i>H. araneus</i> 4 N vs. <i>C. opilio</i> 4 N	0.0149
<i>H. araneus</i> 4 N vs. <i>P. pubescens</i> 4 N	0.0002
$\delta^{15}\text{N}$	
<i>P. pubescens</i> vs. <i>C. opilio</i>	0.0024
4 N vs. 9 N	0.0372
<i>P. pubescens</i> 9 N vs. <i>C. opilio</i> 9 N	0.0001
<i>P. pubescens</i> 9 N vs. <i>P. pubescens</i> 4 N	0.0026

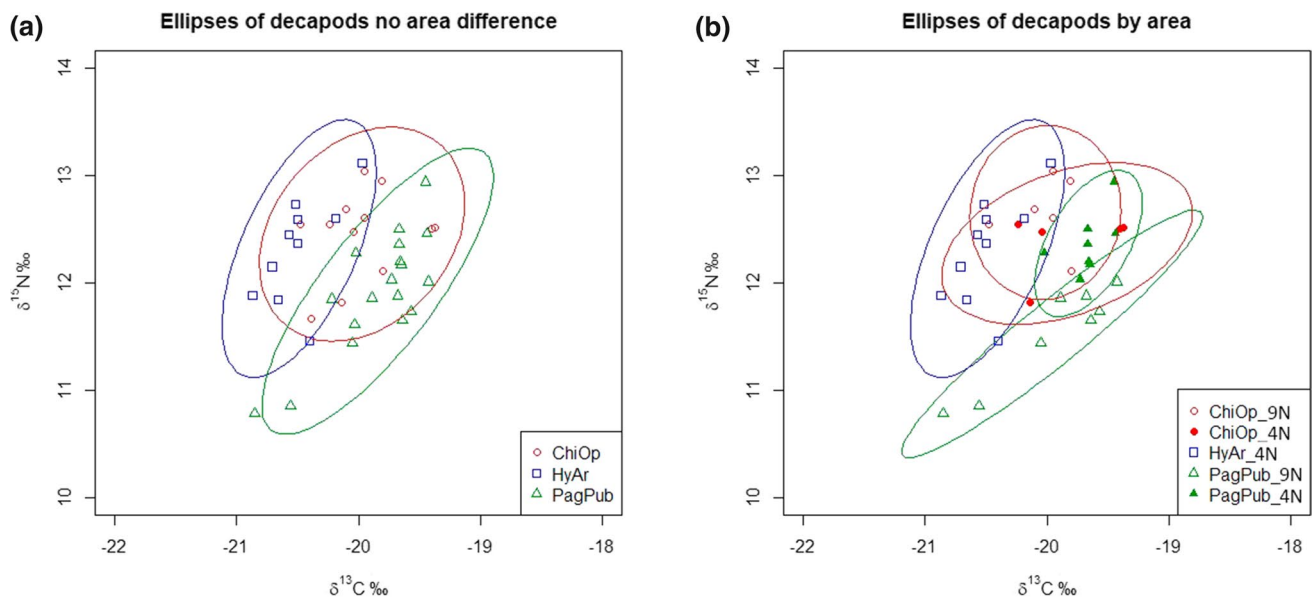


Fig. 6 Ellipses that incorporate 95% of the data, corrected for small sample size (SEA_C) for **a** data not differentiated; **b** data differentiated by sampling area

Table 6 Overlap as the proportion of the non-overlapping area (the total overlap area divided by the sum of the areas of two ellipses minus the total overlap area in $\%^2$) for data with and without area differentiation

	Overlap
<i>C. opilio</i> and <i>H. araneus</i>	0.35
<i>C. opilio</i> and <i>P. pubescens</i>	0.33
<i>H. araneus</i> and <i>P. pubescens</i>	0.08
<i>C. opilio</i> 9 N and 4 N	0.44
<i>P. pubescens</i> 9 N and 4 N	0.12
<i>C. opilio</i> 9 N and <i>P. pubescens</i> 4 N	0.04
<i>C. opilio</i> 4 N and <i>P. pubescens</i> 4 N	0.31
<i>C. opilio</i> 4 N and <i>H. araneus</i> 4 N	0.32
<i>P. pubescens</i> 4 N and <i>H. araneus</i> 4 N	0.03

did not correspond exactly to the dominant macrobenthic species known for the area (*A. borealis*, *A. montagui*, *M. calcarea*, *S. groenlandicus*, *C. ciliatum*). We suspect that this is the result of limitations in taxonomic resolution of visual identification for stomach contents. Only fragments with preserved identifying features (usually hard structures) can be identified to the species level, whereas larger items including most of the bivalve species appear in the form of non-identifiable fragments, generally referred to as bivalve shells.

Observations of the food lumps revealed notable contribution of plant debris to diet compared to other species. This is in agreement with previous studies, i.e. Zmudczyńska-Skarbek et al. (2015) demonstrated that *P. pubescens* can consume plant material of terrestrial origin in the areas of

abundant ornithogenic coastal vegetation in Spitsbergen. Our results show that even in the Pechora Sea, where aquatic vegetation is not abundant (Kucheruk et al. 2003), the diet of *P. pubescens* included a substantial proportion of plant debris.

The pairwise comparison of prey item composition of the three species using Pianka's overlap measure, Bray–Curtis similarity measure and ANOSIM test showed an overlap between the three species with stronger affinity of *C. opilio* and *H. araneus* diets, and slightly different stomach content in *P. pubescens*. We assume that those differences in diets are mainly attributed to the size of prey items as well as differences in claw morphology between Anomura (*P. pubescens*) and Brachyura (*C. opilio* and *H. araneus*). Relatively small sample size available for this study also needs to be taken in consideration and we suggest increasing sample size in the future for more in-depth analyses of the differences in diets of the three species.

The proportional overlap of isotope niches calculated as standard ellipses corrected for small sample size (SEA_C) agrees with some but not all of the results from the ANOVA tests. The ANOVA suggested differences of $\delta^{13}C$ between *H. araneus* and *C. opilio* both with and without area differentiation and $\delta^{15}N$ in *P. pubescens* and *C. opilio* without area differentiation and at 9 N. The standard ellipse calculations took into account both $\delta^{13}C$ and $\delta^{15}N$ data simultaneously whereas ANOVA does not. Therefore we believe that the overlap of SEA_C is a better representation of the trophic niche partitioning by the species.

Limitations of the morphological analyses in feeding studies and further research questions

Several morphological studies of stomach content pointed out limitations of this method. These include low taxonomic resolution and difficulty to assess relative importance of prey items. This is because many prey types remain under-reported due to loss of distinctive diagnostic features as a result of digestion (Tarverdieva 1981; Squires and Dawe 2003). In addition, integrity of the shell fragments can cause bias towards greater contribution of bivalves in food lumps. This limitation of the present study is further complicated by relatively small (especially for *H. araneus*) and temporally restricted samples. Loss of data can also occur from empty stomachs, e.g. in our study 22% of stomachs were excluded from the analyses as empty or near-empty.

However, despite these shortcomings the morphological analysis still allows the assessment of a diversity of prey items in more details than the stable isotope analysis. The morphological analysis revealed that smaller prey items (including foraminifers, hydrozoans, ostracods, nematodes and others) played an important role in the diet of *P. pubescens*, whereas they were absent or scarce in diets of *C. opilio* and *H. araneus*. Larger items including bivalve molluscs *Astarte borealis*, *Serripes groenlandicus* and *Ciliatocardium ciliatum* are available for larger *C. opilio* and *H. araneus*, whilst smaller *P. pubescens* utilise more diverse but poorer in terms of size and biomass infauna. However, for *C. opilio* scooping sand was previously observed by Cunningham (1969) during periods when no larger food was immediately available. Logvinovich (1945) referred to the frequent presence of sediment in the stomachs and intestines of crabs. Foraminifera, minute molluscs and amphipods found in stomach contents probably result from feeding by sieving, as these either burrow in or occur on sediments (Logvinovich 1945).

Literature on the feeding of *C. opilio* also indicates frequent differences in diets of males and females, although this mostly refers to adult crabs (Wieczorek and Hooper 1995; Zakharov et al. 2018). The Pechora Sea however is predominantly populated by subadult males and females which do not differentiate in diets to the same degree (Bakanev et al. 2017) and thus we did not identify sex-related differences in diets in our samples of *C. opilio*.

Microplastics ingestion by decapods in the Pechora Sea

The analysis of inclusions in stomach contents revealed a considerable level of microplastic digestion by all three species. Microplastic particles were present in 35% of *C.*

opilio, 22% of *H. araneus* and 26% of *P. pubescens*. All plastics were classified as microfibers or fragments following Michida et al. (2019). Chemical composition of microplastics was not assessed in the present study although should be addressed in the future specific studies of microplastic digestion to give a better understanding of potential sources of pollution. Consumed microplastics were previously reported for various marine invertebrates including crustaceans, such as the Norway lobster *Nephrops norvegicus* (Murray and Cowie 2011), brown shrimps *Crangon crangon* (Pott 2014), in the gut contents and haemolymph of the shore crab *Carcinus maenas* (Farrell and Nelson 2013) and others. Nevertheless, biological hazards and ecotoxicological effects of digestion of microplastics by marine fauna remain poorly understood. Increased concerns are related to potential adsorption and transport of pollutants through food webs and leaching of industrial additives (i.e. bisphenol A) that are known to have endocrine-disrupting effects (Avio et al. 2017). We suggest that the present study contributes to the knowledge on microplastics distribution and ingestion by benthic fauna. Further studies are needed to reveal the effects of plastics on benthic decapods with specific focus on the effects of digested plastics on the commercially harvested species *C. opilio*.

Conclusions

This study is based on analyses of stomach contents of 75 specimens and stable isotope analyses of 40 specimens of the three benthic decapod species from the Pechora Sea. The study suggests that the invasive snow crab *C. opilio* is in direct trophic competition with the spider crab *H. araneus* and the much smaller hermit crab *P. pubescens*, both of which are native to the Pechora Sea, with the potential to lead to species replacement. *H. araneus* and *P. pubescens* differed in $\delta^{13}\text{C}$, suggesting different food sources, which could be a result of somewhat different prey species composition (i.e. substantial contribution of plant debris in stomach contents of the hermit crabs), and also prey size differences (larger prey items available for *H. araneus*) and differences in claw morphology. The invasive species *C. opilio* had an overlapping isotopic niche as well as overlapping stomach content composition with both of the native decapod species. To understand the extent to which the new competitor may alter the future biodiversity and ecosystem functioning of the Pechora Sea, a long-term study of biodiversity is now needed. This should also include monitoring of the content of microplastics in the stomachs of benthic invertebrates and incorporating these findings into marine environmental management approaches.

Acknowledgements Samples analysed in the present work were collected during the RV Kartesh cruises to the Pechora Sea in 2017 and 2018 and the authors are grateful to LMSU MRC for organising the cruises and to the RV *Kartesh* Captain and crew for their excellent work. The help of taxonomic experts in verifying identifications of animal fragments from the stomach contents is gratefully acknowledged: Anna Tikhonova, IO RAS (foraminifers); Uliana Simakova, IO RAS (macrophytes); Natalia Budaeva, University of Bergen (polychaetes); Maria Mardashova, LMSU MRC (molluscs, polychaetes); Glafira Kolbasova, LMSU MRC (polychaetes). The authors are also grateful to Dr. Andrey Gebruk, Nadia Jogee and anonymous reviewers for helpful feedback. This study was partly supported by RFBR Grant #18-05-60053

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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